E-ARTICLE

Effects of Predator Avoidance Behavior on the Coexistence of Competing Prey

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ABSTRACT: Predator avoidance behavior, in which prey limit foraging activities in the presence of predation threats, affects the dynamics of many ecological communities. Despite the growing theoretical appreciation of the role predation plays in coexistence, predator avoidance behavior has yet to be incorporated into the theory in a general way. We introduce adaptive avoidance behavior to a consumer-resource model with three trophic levels to ask whether the ability of prey—the middle trophic level—to avoid predators alters their ability to coexist. We determine the characteristics of cases in which predator avoidance behavior changes prey coexistence or the order of competitive dominance. The mechanism underlying such changes is the weakening of apparent competition relative to resource competition in determining niche overlap, even with resource intake costs. Avoidance behavior thus generally promotes coexistence if prey partition resources but not predators, whereas it undermines coexistence if prey partition predators but not resources. For any given case, the changes in the average fitness difference between two species resulting from avoidance behavior interact with changes in niche overlap to determine coexistence. These results connect the substantial body of theoretical work on avoidance behavior and population dynamics with the body of theory on competitive coexistence.

Keywords: predator avoidance, antipredator, nonconsumptive effect, coexistence, predation, competition.

Introduction

The complex behaviors of animals in response to their habitat, resources, and threats affect population dynamics (Charnov et al. 1976; Abrams 1992*a*, 1992*b*; Abrams and Vos 2003; Křivan and Sirot 2004) and interspecific interactions (Abrams 2000; Bolker et al. 2003). Behaviors therefore have the potential to alter biological diversity. In particular, behaviors that affect the fundamental interactions between predation and resource competition may alter coexistence of similar species (Chesson and Kuang 2008). We consider here how predator avoidance, in which a species reduces its vulnerability to predation at a cost to its foraging, affects species coexistence in a system where the focal species may partition resources but also may be affected differently by shared natural enemies. Such differential patterns of resource use and predator attack may jointly and separately contribute to species coexistence (Chesson and Kuang 2008).

Similarities in how competition and predation affect species coexistence have long been appreciated (Holt 1977, 1984; Kotler and Holt 1989; Holt et al. 1994) but recently have been explored in more detail (Křivan 2003; Chesson and Kuang 2008; Kuang and Chesson 2010). The key to coexistence is the relative strength of intraspecific density dependence to interspecific density dependence (Chesson 2000, 2018). Both predation and competition contribute to density dependence in multispecies communities (Holt 1977). A form of density dependence such as generalist predation contributes equally to intraspecific and interspecific density dependence. Generalist predation can therefore lower the overall ratio of intraspecific to interspecific density dependence provided by another mechanism, such as resource partitioning. In such cases predation weakens or even destroys stable coexistence (Chesson and Kuang 2008). By contrast, when the focal community has multiple predators that discriminate between their prey species—that is, are at least partly specialized—and so partition their prey, intraspecific density dependence can be intensified relative to interspecific density dependence by predation, thus promoting or strengthening stable coexistence (Chesson and Kuang 2008). Frequency-dependent predation can also have this effect and requires only a single predator species that attacks all species in the focal community (Murdoch et al. 1975; Roughgarden and Feldman 1975; Křivan 2003; Kuang and Chesson 2010).

Although these issues are complex, in the simplest cases where both density-dependent predation and resource com-

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petition are present, the ratio of intra- to interspecific density dependence is intermediate between the ratio that applies for each mechanism alone (Chesson and Kuang 2008; Kuang and Chesson 2010). Therefore, the addition of predation that favors a weaker ratio of intra- to interspecific density dependence than resource competition will in straightforward cases weaken coexistence overall in that community. Conversely, when predators more strongly partition their prey than the prey partition resources, predation is likely to strengthen coexistence in that focal prey community. Although historically predation has often been thought to weaken the effects of competition and thereby promote coexistence (Gurevitch et al. 2000), whether predation strengthens or weakens coexistence depends on how it generates intra- to interspecific density dependence relative to other mechanisms that might be present such as resource competition (Chase et al. 2002; Chesson and Kuang 2008).

Behavioral responses to predators have the potential to greatly alter the critical density-dependent processes for species coexistence (Kotler and Holt 1989). Predator avoidance behavior is increasingly seen as an important determinant of predator-prey dynamics (Peckarsky et al. 2008), trophic cascades (Abrams 1992*b*; Beckerman et al. 1997; Schmitz et al. 2004; Breviglieri et al. 2017), nutrient cycling (Schmitz 2008), evolutionary dynamics (Abrams and Chen 2002*a*; Cressman and Garay 2009), and community diversity and stability (Křivan and Schmitz 2004; Garay-Narvaez and Ramos-Jiliberto 2009). Avoidance behavior is a major category of nonlethal or nonconsumptive effects of predators, sometimes also called trait-mediated indirect interactions with predators (Bolker et al. 2003; Werner and Peacor 2003). Any antipredator strategy that reduces attack rates (Lima 1998)—such as lower foraging activity (Elgar 1989; Werner 1991), use of lower quality habitat (Beckerman et al. 1997), or development of morphological defensive structures (Dahl and Peckarsky 2002; Flenner et al. 2009; Gilbert 2011)—can have negative effects on the prey's growth and reproduction (Pernthaler et al. 1997; Dahl and Peckarsky 2002; Flenner et al. 2009; McCauley et al. 2011). Even transient behavior at the individual level can affect population dynamics (Křivan and Sirot 2004). The threat of predation alone can reduce prey abundance or population growth rate by as much as lethal predation (Werner 1992; Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005) because of trade-offs that reduce foraging rates or other effects, such as stress responses. A potential consequence of reduced growth rates on coexistence is weakening of density-dependent feedback to the focal species through resources. At the same time, these phenomena reduce the benefit that predators gain from their prey species, altering the nature of density-dependent feedback through predators. The effects on species coexistence depend on the net outcomes for the ratio of intraspecific to interspecific density dependence.

Much of the theoretical literature on the community-level effects of predator avoidance behavior has focused on its effects on stability of community dynamics and prey persistence (Abrams 1992*a*, 1992*b*; Abrams and Vos 2003; Bolker et al. 2003; Garay-Narvaez and Ramos-Jiliberto 2009). Predator avoidance has been found most often to stabilize simple models, although that stability declines with the complexity of the model (Bolker et al. 2003). In models including explicit dispersal, predator-driven dispersal can alter the competition-colonization trade-off and may promote or undermine coexistence depending on the circumstances (Orrock et al. 2008). In some empirical systems, avoidance behavior increases resource partitioning and strengthens coexistence, for example, when a *Daphnia* species that is a dominant competitor migrates to a greater depth in the water column to avoid predation by fish, freeing up resources for the less competitive *Daphnia* (Leibold 1991). In others, such as tadpoles reducing their activity to avoid detection by dragonfly larvae, it creates trade-offs between predation risk and the cost of avoidance that can change the outcome of competitive dominance (Werner 1991). The challenge is to find general understanding of when these various outcomes will occur.

We address this challenge by incorporating predator avoidance into a general consumer-resource model with multiple species at each of three trophic levels, with a view to understand the effects of this behavior on the coexistence of consumer species. The kind of situation that we have in mind is perhaps exemplified by stickleback communities in English low-land streams. For example, three-spined (*Gasterosteus aculeatus*) and nine-spined (*Pungitius pungitius*) sticklebacks co-occur and partially overlap in resources, such as their diet and microhabitat preferences, and partially overlap in the set of fish and birds that attack them (Copp and Kovac 2003; Hart 2003). These sticklebacks exhibit costly but adaptive avoidance behavior, such as hiding under plants (Alvarez and Bell 2007; Dingemanse et al. 2007), that reduces predation at the expense of decreasing foraging for cladocerans and other invertebrates (Ward et al. 2004). A similar example would be multiple species of pocket mice (genus *Chaetodipus*) that co-occur in the North American deserts (Price and Brown 1983). These quadrupedal heteromyids are more likely to spend time under sheltering vegetation (Sommers and Chesson 2016), especially in response to the presence of owls that prey on them (Brown et al. 1988), potentially limiting their foraging efficiency and energy intake (Reichman 1979; Price and Reichman 1987; Brown et al. 1988). Although models demonstrate that predator avoidance behavior that is not adaptive and actually leads to extinction could evolve (Matsuda and Abrams 1994), we focus on the effects of avoidance behavior that benefits the focal species, as we might expect to find such behavior persisting in extant natural communities.

Adaptive avoidance behavior by definition provides an intraspecific fitness advantage, but it is unclear when a

species-level average fitness advantage will accrue relative to other species. Whether a species with avoidance behavior excludes an undefended competitor depends on how much of an advantage it gains and how great the stabilizing forces—such as resource or predator partitioning—are in that community (Chesson 2000; Chesson and Kuang 2008). We consider only fixed levels of avoidance in the presence of predators rather than more plastic avoidance that responds to relative densities of predators and resources. This represents a typical response to ambush predators whose density cannot be ascertained by the prey, such as grasshoppers foraging in the presence of ambush spiders (Schmitz 2008) or sticklebacks hiding under plants to avoid herons. Populations of sticklebacks have been shown to differ on average even under laboratory conditions in their level of avoidance of heron attacks, and the level of avoidance is even heritable (Bell 2005), making this an ecologically plausible model and one whose results can then be further generalized. The model may furthermore apply to a variety of morphological defenses that are induced but not particularly labile and thus do not respond rapidly to density, such as bacteria (Pernthaler et al. 1997), rotifers (van der Stap et al. 2008), dragonfly larvae (Flenner et al. 2009), or exposed mayfly larvae (Dahl and Peckarsky 2002) that grow costly filaments or spines in the presence of predators. We find that even such simple responses have major implications for species coexistence.

The Model

Adaptive Avoidance in a General Consumer-Resource Model

We consider a general model for a focal guild of species with densities $\mathbf{N}_j$ $(j = 1, \ldots, J)$ competing for resource species R_l $(l = 1, \ldots, L)$ but also vulnerable to attack by predators P_q $(q = 1, \ldots, Q)$ (table 1). Species j gains the per capita benefit $H_j(\mathbf{R})$ (net harvesting rate) from foraging for resources and per capita risk from predation $\mu_j(\mathbf{P})$, where H_j and μ_j are simply arbitrary increasing functions, respectively, of the vectors of resource ($\mathbf{R}$) and predator ($\mathbf{P}$) densities. Finally, each species j is assumed to have a density-independent mortality rate m_j in addition to predation mortality. The parameter m_j is commonly referred to as the maintenance requirement because it defines the minimum gains from harvesting resources needed to balance mortality. Note that harvesting activity can be assumed to elevate the metabolic rate above the basal rate and may also be accompanied by higher risks of mortality separate from predation risks. The net harvesting rate $H_j(\mathbf{R})$ can therefore be assumed to represent a net outcome of gains from resource intake minus losses from the additional activity involved in foraging above the basal rate m_j. Combining these various effects, we express the per capita growth rate of species j as

$$\frac{1}{N_j}\frac{dN_j}{dt} = H_j(\mathbf{R}) - \mu_j(\mathbf{P}) - m_j. \tag{1}$$

In its simplest form, avoidance behavior is present whenever predators are present but does not depend on predator abundance. We assume this simple situation throughout our analysis. For this case, we introduce a constant f_j to indicate the relative vulnerability of species j to predation with predator avoidance behavior. It is the ratio of predation mortality with and without avoidance behavior. Thus, $f_j < 1$ if avoidance behavior does indeed reduce mortality, and f_j is zero if predation mortality is eliminated entirely by the behavior. Similarly, each species has a constant g_j for the relative efficiency of foraging with avoidance behavior. It is the ratio of net resource gains with and without avoidance behavior. Thus, g_j is equal to 1 if there are no resource costs to avoidance, and lower values mean higher costs. A small f_j/g_j ratio therefore indicates low vulnerability to predation relative to the energetic cost of lost foraging or highly effective avoidance behavior. With these definitions, avoidance behavior changes equation (1) to give

$$\frac{1}{N_j}\frac{dN_j}{dt} = g_j H_j(\mathbf{R}) - f_j\mu_j(\mathbf{P}) - m_j. \tag{2}$$

For this behavior to be adaptive, an individual exhibiting the behavior must be able to invade a population of nonavoiders. If we assume that the system comes to a stable equilibrium, at the resource and predator densities without avoidance behavior ($\mathbf{R}^*_{\text{na}}$ and $\mathbf{P}^*_{\text{na}}$), comparison of equations (1) and (2) shows that a rare invader of species j will have higher fitness than nonavoiding residents—that is, has a higher per capita growth rate—when $(1 - g_j)H_j(\mathbf{R}^*_{\text{na}}) < (1 - f_j)\mu_j(\mathbf{P}^*_{\text{na}})$. This condition simply means that the per capita costs of avoidance to resource consumption are less than the per capita gains from the reduction in predation. Rearrangement of this inequality leads to the following equation for predator avoidance behavior to be adaptive for species j:

$$\frac{1 - g_j}{1 - f_j} < \frac{\mu_j(\mathbf{P}^*_{\text{na}})}{H_j(\mathbf{R}^*_{\text{na}})}. \tag{3}$$

In drawing this conclusion, it has not been necessary to specify the dynamics of the predators and resources. A critical assumption, however, is a globally stable joint equilibrium for the focal guild, predators, and resources in the absence of avoidance behavior, which justifies comparing avoiding and nonavoiding fitnesses only at the nonavoidance equilibrium values ($\mathbf{R}^*_{\text{na}}$ and $\mathbf{P}^*_{\text{na}}$) for the resources and predators. Since equilibrium means zero per capita growth, equation (1) implies $H_j(\mathbf{R}^*_{\text{na}}) = \mu_j(\mathbf{P}^*_{\text{na}}) + m_j$, where all terms are positive. Thus, $H_j(\mathrm{R}^*_{\text{na}}) > \mu_j(\mathbf{P}^*_{\text{na}})$, which means that the right-hand side of equation (3) is <1, and so $f_j < g_j$, whenever avoidance behavior is adaptive. However, this is merely a necessary con-

Table 1: Summary of variables

Variable	Definition	Formula in Lotka-Volterra model, relationship with other parameters
N_j	Density of focal species j	
R_l	Density of a resource l	
P_q	Density of a predator q	
$H_j(\mathbf{R})$	Harvest function of resources $\mathbf{R}$ by focal species j	$\sum_{l=1}^{L} c_{j,l} v_l R_l$
$\mu_j(\mathbf{P})$	Attack function on focal species j by predators $\mathbf{P}$	$\sum_{q=1}^{Q} a_{j,q} P_q$
$H_{j,\max}$	Maximum harvest for focal species j, evaluated in the absence of density dependence	$\sum_{l=1}^{L} c_{j,l} v_l K_l^{\mathrm{R}}$
$\mu_{j,\min}$	Minimum vulnerability to predators for focal species j, evaluated in the absence of density dependence	$\sum_{q=1}^{Q} a_{j,q} K_q^{\mathrm{P}}$
m_j	Density-independent mortality or maintenance requirement of focal species j	
f	Constant reduction in attack function due to avoidance	$0 < f < g$
g	Constant reduction in harvest function due to avoidance	$f < g < 1$
$\mathbf{R}^*_{\mathrm{na}}$, $\mathbf{P}^*_{\mathrm{na}}$	Equilibrium density of resources and predators in the absence of focal species' avoidance behavior	$\mathbf{R}^*_{\mathrm{na}} = \frac{r_l^{\mathrm{R}} - \sum_{j=1}^{J} c_{j,l} N_j}{r_l^{\mathrm{R}} \alpha_l^{\mathrm{R}}}$, $\mathbf{P}^*_{\mathrm{na}} = \frac{r_q^{\mathrm{P}} + \sum_{j=1}^{J} a_{j,q} w N_j}{r_q^{\mathrm{P}} \alpha_q^{\mathrm{P}}}$
$c_{j,l}$	Consumption rate of resource l by focal species j in Lotka-Volterra model	
v_l	Conversion of resource l into focal species biomass in Lotka-Volterra model	
$a_{j,q}$	Attack rate of focal species j by predator q in Lotka-Volterra model	
w	Conversion of focal species into predator biomass in Lotka-Volterra model	
α	Intrinsic density dependence of resource l (α_l^{R}) and of predator q (α_q^{P}) in Lotka-Volterra model	$\alpha_l^{\mathrm{R}} = \frac{1}{K_l^{\mathrm{R}}}$, $\alpha_q^{\mathrm{P}} = \frac{1}{K_q^{\mathrm{P}}}$
K	Carrying capacity of resource l (K_l^{R}) in absence of consumption and of predator q (K_q^{P}) in absence of focal species in Lotka-Volterra model	$K_l^{\mathrm{R}} = \frac{1}{\alpha_l^{\mathrm{R}}}$, $K_q^{\mathrm{P}} = \frac{1}{\alpha_q^{\mathrm{P}}}$
r	Intrinsic regeneration rate of resources (r_l^{R}) and of predator q ($r_q{}^{\mathrm{P}}$) in Lotka-Volterra model	
ρ	Niche overlap between two species of both resources and predators	$\frac{s_{1,2}^{\mathrm{R}} + s_{1,2}^{\mathrm{P}}}{\sqrt{(s_{1,1}^{\mathrm{R}} + s_{1,1}^{\mathrm{P}})(s_{2,2}^{\mathrm{R}} + s_{2,2}^{\mathrm{P}})}}$
ρ^{R}, ρ^{P}	Niche overlap between two species in resources ρ^{R} or in predators ρ^{P} only	$\rho^{\mathrm{R}} = \frac{s_{1,2}^{\mathrm{R}}}{s_1^{\mathrm{R}} s_2^{\mathrm{R}}}$, $\rho^{\mathrm{P}} = \frac{s_{1,2}^{\mathrm{P}}}{s_1^{\mathrm{P}} s_2^{\mathrm{P}}}$
κ_j	Average fitness of focal species j	$\frac{1}{s_j}\left(\sum_{l=1}^{L} g_j c_{j,l} K_l^{\mathrm{R}} v_l - \sum_{q=1}^{Q} f_j a_{j,q} K_q^{\mathrm{P}} - m_j\right)$
φ_j	Ratio of sensitivity of focal species j to predation relative to resource competition	$\frac{s_j^{\mathrm{P}}}{s_j^{\mathrm{R}}}$
$\varphi_{j,\mathrm{na}}$	Ratio of sensitivity of focal species j to predation relative to resource competition of a nonavoiding focal species $j_{,\mathrm{na}}$	$\frac{s_{j,\mathrm{a}}^{\mathrm{P}}}{s_{j,\mathrm{a}}^{\mathrm{R}}} = \frac{f_j}{g_j}\left(\frac{s_{j,\mathrm{na}}^{\mathrm{P}}}{s_{j,\mathrm{na}}^{\mathrm{R}}}\right)$
$\mathrm{S_j}$	Sensitivity of focal species j to resources and predators due to density dependence	$s_j = \sqrt{s_{j,j}} = \sqrt{\left(g_j^2 \sum_l \frac{c_{j,l}^2 v_l}{r_l^{\mathrm{R}} \alpha_l^{\mathrm{R}}} + f_j^2 \sum_q \frac{a_{j,q}^2 w}{r_q^{\mathrm{P}} \alpha_q^{\mathrm{P}}}\right)}$
s_j^{P}, s_j^{R}	Sensitivity of focal species j to resources only (s_j^{R}) and predators only (s_j^{P}) due to density dependence	$s_j^{\mathrm{R}} = \sqrt{g_j^2 \sum_l \frac{c_{j,l}^2 v_l}{r_l^{\mathrm{R}} \alpha_l^{\mathrm{R}}}}$, $s_j^{\mathrm{P}} = \sqrt{f_j^2 \sum_q \frac{a_{j,q}^2 w}{r_q^{\mathrm{P}} \alpha_q^{\mathrm{P}}}}$

dition for the adaptiveness of avoidance behavior. Equation (3) defines the full sufficient conditions. Note also that equation (3) asks only whether specific avoidance behavior is adaptive relative to nonavoidance, not whether it is optimal in some sense, or an evolutionarily stable strategy. For these considerations, constraints and trade-offs would need to be specified. However, we can analyze the effects of avoidance behavior on coexistence without making such specifications. Thus, we can derive conclusions from the effect of avoidance behavior regardless of whether the behavior happens to optimal, as further detailed in "Discussion."

Note finally that equation (3) for avoidance behavior being adaptive applies only to the equilibrium density of nonavoiders and constrains no other situation. For the Lotka-Volterra model that follows, equation (3) can be reinterpreted in terms of niche overlap between avoiders and nonavoiders (app. B; apps. A–C are available online), similar to their roles in species coexistence.

A Tritrophic Lotka-Volterra Model

We now ask how adaptive avoidance behavior, as defined by equation (3), affects coexistence of species in the focal guild. For this we need to specify the dynamics of resources and predators in addition to the dynamical equations for the focal guild. We use the three-trophic-level community model of Chesson and Kuang (2008), which gives simple analytical results for the interaction between predation-based and competition-based species coexistence mechanisms. Being a Lotka-Volterra model, the functions $H_j(\mathbf{R})$ and $\mu_j(\mathbf{P})$ are linear, and equation (2) becomes

$$\frac{1}{N_j}\frac{dN_j}{dt} = \underbrace{\sum_{l=1}^{L} c_{j,l}\nu_l R_l - m_{c,j}}_{H_j(\mathbf{R})} - \underbrace{\sum_{q=1}^{Q} a_{j,q}P_q}_{\mu_j(\mathbf{P})} - m_j. \tag{4}$$

Here, $c_{j,l}$ is the consumption rate on resource l by consumer j, ν_l is the conversion of consumed resource l into consumer, $m_{c,j}$ is the loss from elevation in the metabolic rate due to resource capture, and $a_{j,q}$ is the attack rate on consumer j by predator q. The resources are assumed to be self-renewing, with logistic growth rates modified by losses due to consumption by the focal guild to give the equation

$$\frac{1}{R_l}\frac{dR_l}{dt} = r_l^{\mathrm{R}}(1 - \alpha_l^{\mathrm{R}}R_l) - \sum_{j=1}^{J} c_{j,l}N_j. \tag{5}$$

The predator dynamics are represented by logistic growth increased by consumption of focal consumers, which the predator converts to new biomass at rate w:

$$\frac{1}{P_q}\frac{dP_q}{dt} = r_q^{\mathrm{P}}(1 - \alpha_q^{\mathrm{P}}P_q) + \sum_{j=1}^{J} a_{j,q}wN_j. \tag{6}$$

Appendix A shows that a Lyapunov function exists for this system of equations, which shows that whenever the system has a positive equilibrium for the focal consumer species, resources, and predators, it is globally stable.

The presence of logistic growth in the predator equation (6) means the predators have resources outside the focal guild potentially because of spatial-scale differences between the predator guild and focal guild. These resources mean that the predators cannot become extinct from the system yet still respond to the densities of the focal guild providing density-dependent feedback loops between the focal guild and the predator guild. For simplicity of analysis, we assume also that the resources in the model do not become extinct. This assumption is discussed in detail in appendix A, where sufficient conditions for its validity are derived. These conditions restrict how much the consumption rates of different resources can differ, taking into account their replenishment rates and the maintenance requirements of the consumers. As first discussed by Abrams (1998), high-maintenance requirements minimize these restrictions. It is not difficult to generalize beyond these restrictions (Chesson and Kuang 2008), but it is then necessary to consider community assembly processes that go beyond the dynamical equations themselves (as explained in "Discussion"), while the key conclusions here do not require it. Given these assumptions, analysis of the equations reduces to determining when the focal consumer species have a positive equilibrium (app. A).

To modify the dynamical equations (4)–(6) to include predator avoidance behavior according to equation (2), $c_{j,l}$ is multiplied by g_j and $a_{j,q}$ is multiplied by f_j. The resulting equations are equivalent to the original model, with parameter values modified by the effects of avoidance behavior. Thus, the analytic results for this model derived by Chesson and Kuang (2008) apply both with and without avoidance behavior, differing only in parameter values. Chesson and Kuang (2008) show that coexistence conditions for a two-species focal guild can be conveniently summarized in terms of just two quantities, niche overlap ρ and the average fitness ratio κ_1/κ_2 of species 1 and 2, defined in terms of the parameters of the model. Niche overlap is a measure of the relative sensitivity of each species to limitations by their various resources and predators on the basis of their harvest of and vulnerability to each. The average fitness of a species is a measure of net harvest after losses, scaled by the species' joint sensitivity to predation and competition. For full details, see appendix A.

The critical ratios of interspecific to intraspecific competition, α_{12}/α_{22} (interspecific competition of species 2 on species 1 relative to intraspecific competition of species 2 on itself) and α_{21}/α_{11} (interspecific competition of species 1 on species 2 relative to intraspecific competition of species 1 on itself), are related to average fitness ratios and niche overlap according to the equations

$$\frac{\alpha_{12}}{\alpha_{22}} = \frac{\kappa_2}{\kappa_1}\rho,$$
$$\frac{\alpha_{21}}{\alpha_{11}} = \frac{\kappa_1}{\kappa_2}\rho \tag{7}$$

(Chesson and Kuang 2008). The necessary and sufficient condition for stable coexistence between species 2 and species 1 is that these ratios are both <1. Algebraic rearrangement leads to the equivalent condition

$$\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho}. \tag{8}$$

In other words, for the two species to coexist, the ratio of their average fitnesses must lie between the niche overlap measure ρ and its reciprocal. The lower the niche overlap, the greater the average fitness difference can be (i.e., the more their ratio can deviate from 1) while still permitting coexistence. When the two species have nearly complete niche overlap, they will coexist only when their average fitnesses are very similar. On the other hand, two species with no overlap in predators or resources can coexist despite having very different average fitness.

Overall niche overlap ρ includes both resource overlap ρ^{R} and predator overlap ρ^{P} (fig. 1). Any two focal species may mostly overlap in their limiting resources (fig. 1*a*), may be limited primarily by distinct resources and hence little overlap (fig. 1*c*), or have intermediate overlap in their limiting resources (fig. 1*b*). For example, granivorous rodents that are complete generalists may overlap completely in the size and type of seeds they consume (fig. 1*a*), while in more productive environments other rodents may partially partition seeds they primarily select on the basis of size (Brown and Lieberman 1973) or because of differential toxicity (e.g., jojoba seeds for Bailey's pocket mouse; Sherbrooke 1976; fig. 1*b*, 1*c*). Similarly, the focal species may be primarily limited by the same set of predators (fig. 1*c*) or by distinct predators (fig. 1*a*). For example, three-spined and nine-spined sticklebacks may both be preyed on by pike and perch (Hoogland et al. 1956), creating high predator overlap if those are the only fish in their stream (fig. 1*c*), but the smaller spines of the nine-spined species may additionally make them vulnerable to fish with smaller gapes that cannot eat three-spined sticklebacks, creating some reduction in overlap (fig. 1*b*). How ρ^{R} and ρ^{P} combine to give the overall niche overlap ρ depends on the relative sensitivities φ_j of each focal species j to competition and predation, which depends on the strengths of the intraspecific feedback loops through predators and resources (app. A). Then overall niche overlap between species 1 and 2 can be represented in terms of ρ^{R} and ρ^{P} as follows (app. A):

$$\rho = \frac{\rho^{\mathrm{R}}}{\sqrt{(1+\varphi_1^2)(1+\varphi_2^2)}} + \frac{\rho^{P}}{\sqrt{(1+\varphi_1^{-2})(1+\varphi_2^{-2})}}. \tag{9}$$

Finally, we need the average fitnesses κ_j, which from Chesson and Kuang (2008) are defined as

$$\kappa_j = \frac{1}{s_j}(H_{j,\max} - \mu_{j,\min} - m_j), \tag{10}$$

where $H_{j,\max}$ and $\mu_{j,\min}$ are the maximum H_j and minimum μ_j, respectively, which are achieved at zero densities of each of the species, freeing them of competition and apparent competition (app. A). Their difference is scaled by the sensitivity s_j of species j to density dependence through resources and predators (app. A). How the κ's and ρ change with avoidance behavior determine its effect on coexistence according to equation (8).

Analysis

Effects of Avoidance Behavior on Niche Overlap

By equation (8), niche overlap ρ puts a constraint on allowable κ ratios compatible with coexistence. Small ρ values mean there is little constraint, favoring coexistence, while large values mean that the κ ratios are highly constrained, making coexistence difficult.

Niche overlap changes in a relatively straightforward way with avoidance behavior. To see this, we define $\varphi_{j,\mathrm{a}}$ as the relative sensitivity to predation relative to competition φ_j with avoidance behavior and $\varphi_{j,\mathrm{na}}$ as relative sensitivity to predation without avoidance. These two quantities are very simply related as

$$\varphi_{j,\mathrm{a}} = \frac{f_j}{g_j}\varphi_{j,\mathrm{na}}, \tag{11}$$

because f and g can be factored out of the relative sensitivity ratio (app. B). In this expression, f/g is an inverse measure of the effectiveness of avoidance behavior because f measures the exposure to predation and g measures the opportunities for foraging. Thus, a small f/g indicates low exposure to predation relative to the opportunities for foraging and so high effectiveness of avoidance. In the figures, the direct measure of avoidance effectiveness is used, which is $1 - f/g = (g-f)/g$. Here $g-f$ is how much higher foraging opportunities are than exposure to predators. Dividing this by g standardizes this measure relative to the foraging opportunities.

Substituting equation (11) into equation (9) for ρ, we obtain the following equation showing how avoidance affects niche overlap:

$$\rho = \frac{\rho^{\mathrm{R}}}{\sqrt{\left[1+\left(\frac{f_1}{g_1}\right)^2\varphi_{1,\mathrm{na}}^2\right]\left[1+\left(\frac{f_2}{g_2}\right)^2\varphi_{2,\mathrm{na}}^2\right]}} + \frac{\rho^{\mathrm{P}}}{\sqrt{\left[1+\left(\frac{f_1}{g_1}\right)^{-2}\varphi_{1,\mathrm{na}}^{-2}\right]\left[1+\left(\frac{f_2}{g_2}\right)^{-2}\varphi_{2,\mathrm{na}}^{-2}\right]}}. \tag{12}$$

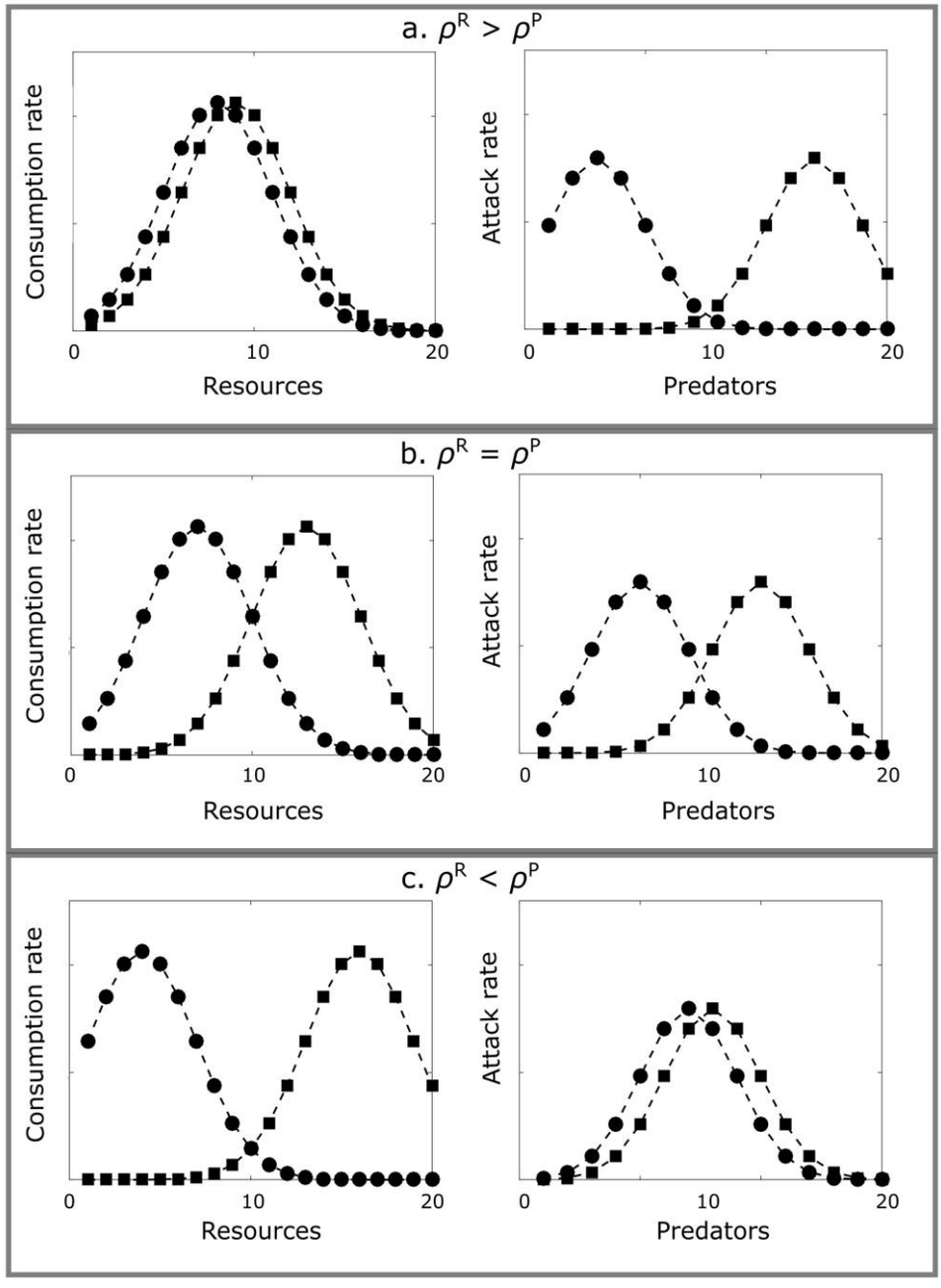

Figure 1: Niche overlap in resources and predators. *a*, The two species overlap more in their consumption of resources than in vulnerability to predator attack ($\rho^P < \rho^R$). *b*, The two species overlap equally in predators and resources ($\rho^P = \rho^R$). *c*, The two species overlap more in predators than in resources ($\rho^P > \rho^R$). Circles = species 1; squares = species 2.

In this equation, the separate niche overlaps ρ^R and ρ^P for resources and predators, respectively, are independent of avoidance behavior. The $\varphi_{j,\mathrm{na}}$ are constants because they are defined in terms of the nonavoidance case. Thus, in equation (12) a decrease in f/g for either species decreases the denominator of ρ^R and increases the denominator of ρ^P, increasing the relative contribution of resource partitioning compared with predator partitioning to overall overlap, ρ. Figure 2 illustrates the resulting changes to the coexistence region (white) defined by equation (8) for the various scenarios of ρ^R and ρ^P illustrated in figure 1 and the sensitivity to predation $\varphi_{j,\mathrm{na}}$. On the *X*-axis is effec-

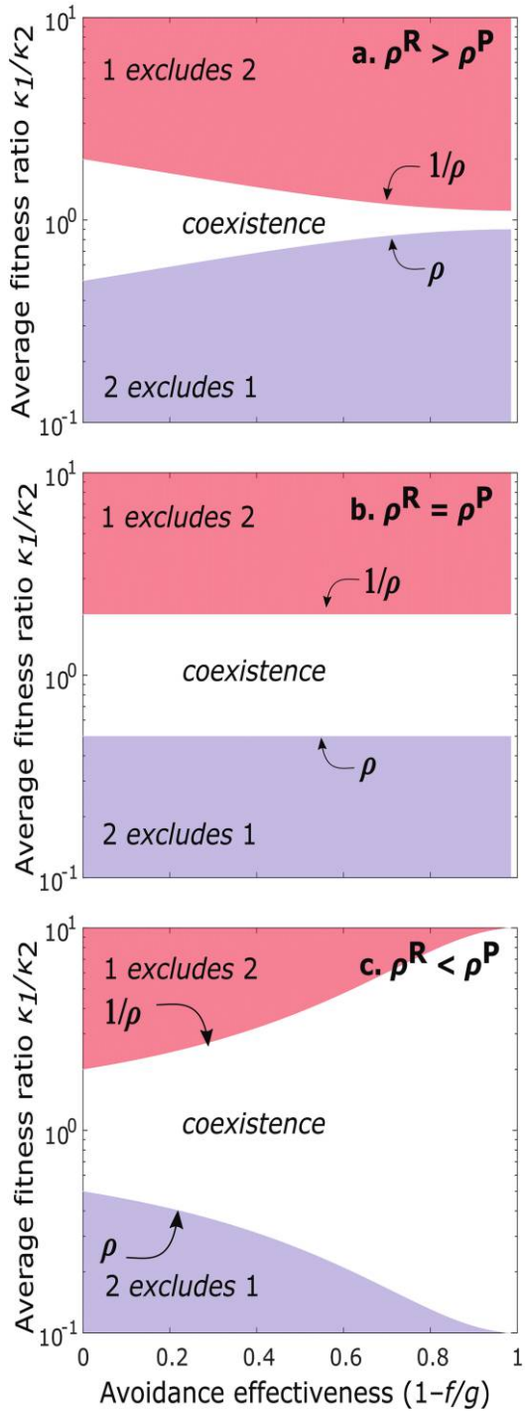

Figure 2: Changes in niche overlap and opportunity for coexistence with avoidance effectiveness. Avoidance effectiveness measures how much predation is reduced relative to loss in foraging opportunities. Colors indicate coexistence regions, as given in equation (11): pink = species 1 dominates; blue = species 2 dominates; white = coexistence occurs. *a*, Greater overlap in resource use than predators ($\rho^R = 0.9$, $\rho^P = 0.1$). *b*, Equal overlap in resource use and predators ($\rho^R = \rho^P = 0.5$). *c*, Less overlap in resource use than predators ($\rho^R = 0.1$, $\rho^P = 0.9$). For all panels, $\varphi = 1$, $g = 0.7$, and f varies from 0.7 down to 0.01.

tiveness of avoidance ($1 - f/g$), assuming that these are the same for the two species for visual clarity. The quantities ρ and $1/\rho$ are the boundaries between the colored regions and white region as indicated. The vertical distance between the colored regions gives the magnitude of the coexistence region for given $1 - f/g$ values in terms of the average fitness ratio (κ_1/κ_2). Thus, the greater this vertical distance, the greater the ease of coexistence in terms of allowable average fitness ratios.

Note that for $\rho^R > \rho^P$ (fig. 1*a*) the magnitude of the coexistence region decreases with effectiveness of avoidance because ρ then increases as a function of the effectiveness of avoidance (fig. 2*a*). Inversely, we see the magnitude of the coexistence region increasing for $\rho^R < \rho^P$ (figs. 1*c*, 2*c*) and not changing when $\rho^R = \rho^P$ (figs. 1*b*, 2*b*). As effectiveness increases, in all cases ρ approaches ρ^R, which defines the coexistence region at 100% effectiveness of avoidance ($f = 0$), meaning the focal species can avoid predation completely while still managing to forage. Naturally, with $f = g$ (or $1 - f/g = 0$), avoidance behavior is ineffective because no foraging gains accrue beyond the level of predation avoided. Then ρ takes the same value as with no avoidance behavior, which defines the coexistence region with effectiveness = 0 in figure 2. When the f/g ratio differs between focal species, the same trends nevertheless apply, as can be seen directly from equation (12). For instance, if f/g is varied for just one of the two focal species, then ρ and the coexistence region change in the same way as when they are equal and vary in tandem, but the magnitude of the change in ρ—and hence the change in the coexistence region—is less.

The magnitude of the change in the coexistence region with avoidance behavior naturally depends on the relative sensitivity to predation $\varphi_{j,\mathrm{na}}$ (eq. [11]). Small φ means that the coexistence region is insensitive to predation and therefore cannot change much with avoidance behavior. On the other hand, large φ means high sensitivity to predation. Correspondingly, large changes in the coexistence region occur as effectiveness of avoidance increases (fig. C1; figs. C1–C3 are available online).

Effects of Avoidance on the Average Fitness Ratio

Although ρ determines the range of average fitness ratios compatible with coexistence, the average fitness ratio itself can be very strongly affected by avoidance behavior. With avoidance behavior, equation (10) implies that the average fitness ratio becomes

$$\frac{\kappa_1}{\kappa_2} = \frac{H_{1,\max,na} - m_1 - m_1\left(\frac{1}{g} - 1\right)}{H_{2,\max,na} - m_2 - m_2\left(\frac{1}{g} - 1\right)} \left\{ \frac{1 - \frac{f}{g}\left[\frac{\mu_{1,\min,na}}{H_{1,\max,na} - m_1 - m_1\left(\frac{1}{g} - 1\right)}\right]}{1 - \frac{f}{g}\left[\frac{\mu_{2,\min,na}}{H_{2,\max,na} - m_2 - m_2\left(\frac{1}{g} - 1\right)}\right]} \right\}. \tag{13}$$

For simplicity, we assume here that the pair of focal species 1 and 2 are equally sensitive to their resources and to their predators. We also assume that their parameters f and g vary in tandem for both species and so are not subscripted in equation (13). Members of many guilds of competing species may be expected to evolve similar avoidance strategies (Adler 1999), making this an ecologically reasonable case to consider for its own sake, but the primary insights are more general than this case alone, as can be seen from the full equation (app. B; eq. [B17]) with species-specific f and g.

As effectiveness of avoidance approaches 100%, that is, f/g approaches zero, the average fitness ratio converges on the following value:

$$\frac{\kappa_1}{\kappa_2} = \left[\frac{H_{1,\max,na} - m_1 - m_1\left(\frac{1}{g} - 1\right)}{H_{2,\max,na} - m_2 - m_2\left(\frac{1}{g} - 1\right)}\right] = \frac{gH_{1,\max,na} - m_1}{gH_{2,\max,na} - m_2}. \tag{14}$$

Understandably, at 100% effectiveness, the average fitness ratio is independent of $\mu_{1,\min,na}$ and $\mu_{2,\min,na}$, which define minimum predation mortality without avoidance behavior. However, the average fitness ratio depends strongly on the harvesting abilities H and maintenance requirements m that apply in the absence of predators. Naturally, $\mu_{1,\min,na}$ and $\mu_{2,\min,na}$ have major effects on κ_1/κ_2 at low effectiveness of avoidance. In fact, with $f/g = 1$, which is equivalent to no avoidance, the average fitness ratio is

$$\frac{\kappa_1}{\kappa_2} = \left[\frac{H_{1,\max,na} - m_1 - m_1\left(\frac{1}{g} - 1\right) - \mu_{1,\min,na}}{H_{2,\max,na} - m_2 - m_2\left(\frac{1}{g} - 1\right) - \mu_{2,\min,na}}\right] = \frac{gH_{1,\max,na} - m_1 - g\mu_{1,\min,na}}{gH_{2,\max,na} - m_2 - g\mu_{2,\min,na}}. \tag{15}$$

These properties are illustrated in figure 3, where κ_1/κ_2 is plotted as a function of effectiveness of avoidance, $1 - f/g$. The different curves are defined by different $\mu_{1,\min,na}$ but converge on the same value at 100% effectiveness because their H and m values are the same. Varying the H and m values also naturally varies the height of the point of convergence at $1 - f/g = 1$ (fig. C3).

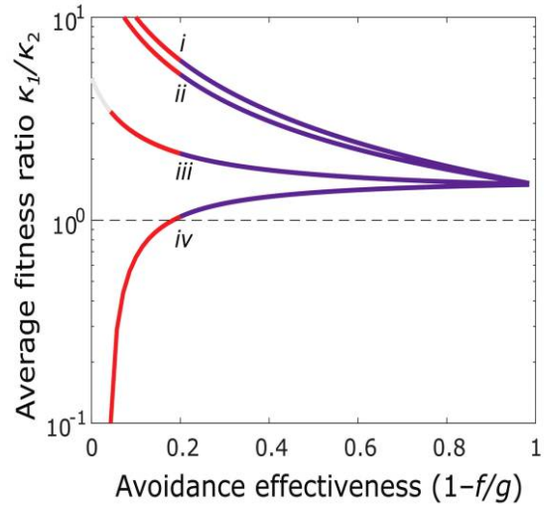

Figure 3: Change in average fitness ratio for different per capita risk of predation for species 1 (μ_1) as a function of avoidance effectiveness. Lines are defined by equation (13), with each $\mu_{1,\max}$ varying from 3.5 to 0.02 between the lowest and highest lines. Purple = avoidance is adaptive for both species; red = avoidance is adaptive for species 1 only; blue (not visible in this parameter space) = avoidance is adaptive for species 2 only; gray = avoidance is adaptive for neither. Dashed line is the 1:1 line of equal average fitness. Parameters: $H_{1,\max} = H_{2,\max} = 5$, $m_1 = 0.5$, $m_2 = 1.5$, $\mu_{2,\min} = 2.7$, $\varphi_1 = \varphi_2 = 1$, $g = 0.7$, and f varies from 0.7 down to 0.01, defining the change along the ineffectiveness axis ($1 - f/g$). *i*, $\mu_{1,\min} = 0.02$; *ii*, $\mu_{1,\min} = 0.8$; *iii*, $\mu_{1,\min} = 3.5$; *iv*, $\mu_{1,\min} = 4.45$.

Whether the average fitness ratio κ_1/κ_2 becomes closer to 1 with avoidance behavior, as figure 3 illustrates, depends on how different the $\mu_{1,\min,na}$ and $\mu_{2,\min,na}$ are relative to other parameters. Inspection of equation (13) (see app. B) shows that the average fitness ratio increases; that is, species 1 benefits more than species 2 from effective avoidance if

$$\frac{\mu_{1,\min,na}}{H_{1,\max,na} - m_1 - m_1\left(\frac{1}{g} - 1\right)} > \frac{\mu_{2,\min,na}}{H_{2,\max,na} - m_2 - m_2\left(\frac{1}{g} - 1\right)}. \tag{16}$$

Thus, the species with the greater vulnerability to predation relative to their net harvest benefits relatively more from effective avoidance behavior. Although this outcome may often lead to average fitnesses becoming closer to 1 (an equalizing effect, sensu Chesson 2000), the opposite outcome is also possible (fig. C3). Note also that the final value (eq. [14] with 100% avoidance effectiveness) is independent of g in the event that m is proportional to H; that is, H/m does not depend on the species. In this case, highly effective avoidance eliminates all effects of predation on species coexistence; that is, there are no consumptive or nonconsumptive effects on coexistence. If the g's differ between species, $1/g - 1$, which is a measure of avoidance effort, must scale in proportion to

$H/m - 1$ for no dependence of final fitness ratio on the magnitude of avoidance (app. B).

The color of the average ratio in figure 3 indicates whether avoidance behavior is adaptive for either or both species in the absence of the other. Inspection of equation (3) for adaptive avoidance behavior reveals that avoidance effectiveness—namely, the relationship between f and g—must meet some minimum value based on the ratio of μ to H for that species in order to be adaptive. Ineffective avoidance behavior is not adaptive for either species, and therefore the lines are gray at the lowest values of effectiveness. The specific minimum effectiveness at which avoidance behavior becomes adaptive differs for each species and depends on their harvest and attack functions (app. B).

The effects of avoidance on coexistence itself are more fully illustrated in figure 4, where the average fitness curves from figure 3 are superimposed over the coexistence regions from figure 2, showing the interaction between niche overlap and average fitness in determining coexistence. The curves all have the same H and m values and so converge on the same value at 100% effectiveness. With these H and m values, species 1 is dominant at 100% avoidance; that is, the average fitness ratio is >1. At 0% effectiveness, however, the fitness ratios are more extreme and vary greater between the four curves because the minimum predation mortalities $\mu_{j,\min,na}$ differ between curves. The extreme variation in curve iv represents inviability of species 1 in the presence of predation without effective avoidance. In these examples, effective avoidance leads to more equal average fitnesses, that is, acts as an equalizing mechanism (Chesson 2000).

When the two species have greater overlap in predators than resources, as in figures 1*c* and 2*c*, the equalizing effect is sufficient to strongly promote coexistence, as shown in figure 4*c*. In figure 4*a*, however, contraction of the coexistence region because resource overlap is greater than predator overlap prevents the average fitness ratios from entering the coexistence region, while in figure 4*b* equal overlap for resources and predators means that the change in the fitness ratio alone determines whether coexistence will occur.

Together, these examples serve to illustrate that average fitness differences can increase or decrease because of more effective predator avoidance. Whether avoidance is equalizing depends on the two species' difference in harvest and maintenance requirements and on which species is more vulnerable to predation (eq. [15]). These examples further serve to illustrate that whether avoidance behavior ultimate alters coexistence depends on an interaction between the change in niche overlap and the change in average fitness differences. Fortunately, general principles determine the outcome of this interaction.

Note that the average fitness ratio depends not only on the ratio of f/g but also on the value of g itself. Because g represents the proportional decrease in foraging due to avoid-

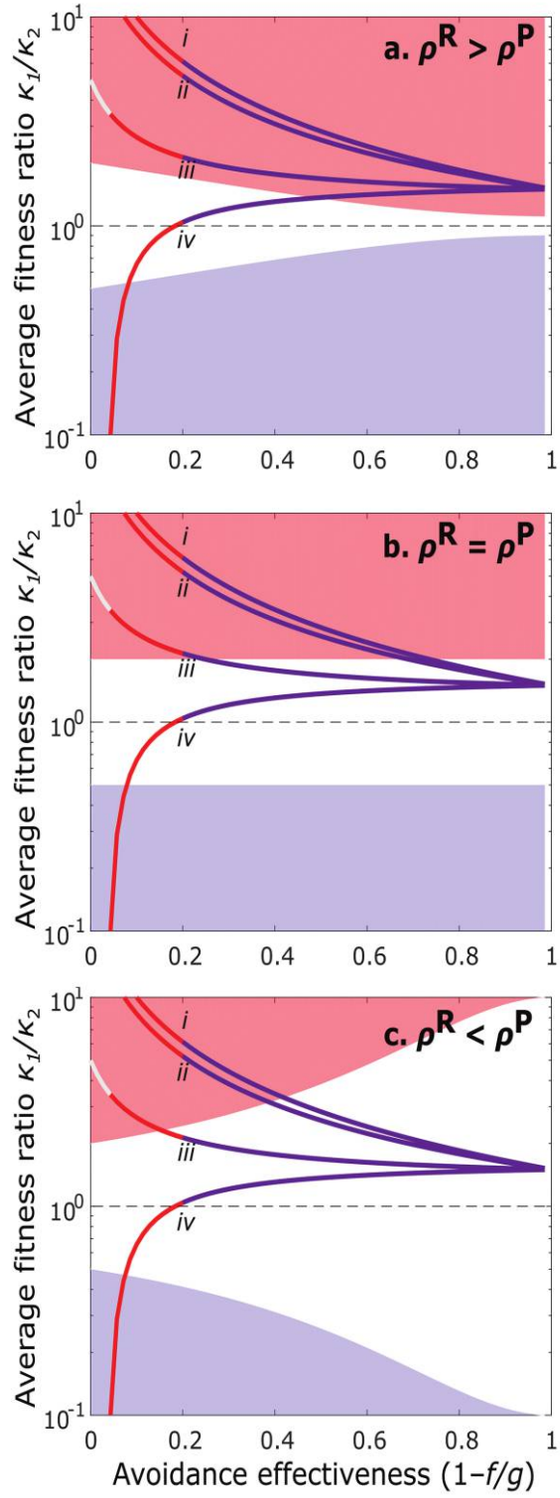

Figure 4: Niche overlap and average fitness ratio interact to determine coexistence. Average fitness ratio curves from figure 3 are overlaid on the coexistence regions from figure 2, with parameters and colors as in figures 2 and 3.

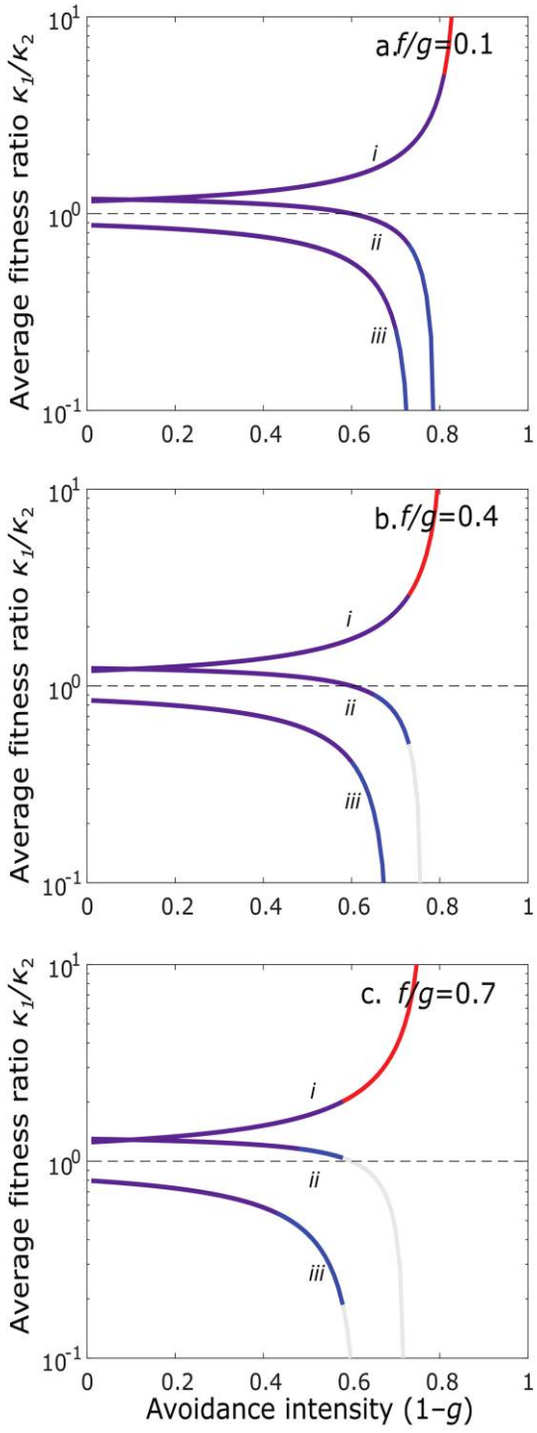

Figure 5: Effect of avoidance intensity on average fitness differences with fixed values of avoidance effectiveness. *a*, $f/g = 0.1$; *b*, $f/g = 0.4$; *c*, $f/g = 0.7$. Lines are defined by equation (13), with each m_1 varying from 0.1 to 2 between the lowest and highest lines (*i–iv*). *i*, $H_{1,\max} = 4$, $m_1 = 0.1$; *ii*, $H_{1,\max} = 5$ $m_1 = 1$; *iii*, $H_{1,\max} = 4$, $m_1 = 1$. Colors indicate values over which avoidance intensity is adaptive: purple = avoidance is adaptive for both species; red = avoidance is adaptive for species 1 only; blue = avoidance is adaptive for species 2 only; gray = avoidance is adaptive for neither. Dashed line is the 1:1 line of equal average fitness. Other parameters: $H_{2,\max} = 4$, $m_2 = 0.6$, $\mu_{1,\min} = \mu_{2,\min} = 2$, $\varphi_1 = \varphi_2 = 1$, and g varies from 0.99 down to 0.2, defining the change along the ineffectiveness axis ($1 - g$).

ance, we can think of it as determining the intensity of avoidance behavior, for example, the fraction of time spent hiding instead of foraging. We can therefore vary a measure of intensity, $1 - g$, while defining f as a constant proportion of g (fig. 5). In varying g, the total energy harvested and incorporated by the focal species clearly must be at least as much as its maintenance requirement m_j in order for the species to persist, so some limit on realistic adaptive values exists. In a very general model such as the Lotka-Volterra model, though, parameters can have a wide range of possibilities depending on how they are interpreted. If m_j is small relative to $H_{\max}$, species j can potentially vary its foraging intensity g over a wide range and still be viable. By rearranging equation (13) (for details, see app. B), we see that with increasingly intense avoidance behavior for both species, the condition for species 1 to benefit relative to species 2 is

$$\frac{m_1}{m_2} < \frac{H_{1\,\max,\mathrm{na}} - m_1 - \frac{f}{g}\mu_{1\,\max,\mathrm{na}}}{H_{2\,\max,\mathrm{na}} - m_2 - \frac{f}{g}\mu_{2\,\max,\mathrm{na}}}. \qquad (17)$$

Fundamentally, the species that benefits in terms of average fitness is the one with the smaller maintenance requirement m relative its net harvesting ability. This result is intuitive because such a species can afford to take time out to forage because its costs during inactivity are low.

Regardless of which competitor benefits from more intense avoidance, the differences in average fitness become greater as foraging slows, provided the relative effectiveness for each species is kept constant. Altering g while holding f/g constant does not alter niche overlap. In particular, this means that low foraging rates without correspondingly high effectiveness of avoidance, that is, high $1 - f/g$, is greatly unfavorable to coexistence because of the high average fitness differences that result. However, these situations in general will not correspond to adaptive avoidance (fig. 5).

Discussion

We have brought together two avenues of theoretical research: how predation affects species coexistence and how its effects on prey behavior affect species coexistence. Although previous studies examined how predator avoidance affects the stability of food chains (DeAngelis et al. 2007) and food webs (Abrams 2004; Garay-Narvaez and Ramos-Jiliberto 2009), the persistence of populations (Abrams 1992*b*; Abrams and

Vos 2003) or metapopulations (Orrock et al. 2008), and the coexistence of prey that share predators but not resources (Abrams and Matsuda 1993, 1997; Abrams et al. 1998), a general understanding of how avoidance behavior affects coexistence of prey species did not emerge. The details of our development may appear complex, but in fact they provide a relatively simple story utilizing the concepts of intensity and effectiveness of avoidance (table 2). We assume that predator avoidance leads to a reduction in the ability of the focal species to forage for resources, and we define the intensity of avoidance as the proportional reduction in foraging activity. We define the effectiveness of avoidance as the relative reduction in predation, accounting for the intensity of avoidance (fig. 2). The bottom line is that effective avoidance reduces—and, in the extreme, all but eliminates—the effect of predators on the interactions between the focal species. Understandably, at 100% effective avoidance, mortality due to predation no longer has a role in species coexistence, but the nonconsumptive effect of induced avoidance behavior (e.g., Preisser et al. 2007; McCauley et al. 2011; Breviglieri et al. 2017) may differentially affect the species, altering the outcome of their interactions.

The details of our results can be understood in terms of the effects of avoidance behavior on the niche overlap between two focal species (measured by the quantity ρ) and their average fitness comparison (κ_1/κ_2). In our Lotka-Volterra model, coexistence occurs when ρ is small enough to counteract the effect of species average differences measured as κ_1/κ_2 (eq. [7]). Both ρ and κ_1/κ_2 are affected by avoidance behavior, and disentangling their joint changes with avoidance behavior can be complex. However, the behavior of the niche overlap measure is relatively straightforward and paints the broad picture. The niche overlap measure can be understood as defining the breadth of average fitness differences allowing coexistence. Average fitnesses depend on a great many factors beyond avoidance behavior, and ρ defines the overall constraints on this constellation of factors compatible with coexistence. In this sense, ρ defines the ease with which coexistence occurs separately from the effects of avoidance behavior on the average fitness ratio (table 2).

The niche overlap measure weights every component of the shared environment of the focal species by the degree to which a component (here a resource or predator species) limits the focal species in a density-dependent way, where we mean density dependence in the multispecies sense of the effect of the density of any focal species on any other focal species (Chesson 2003). Thus, if a component is only a weak mediator of density dependence, it is weighted only weakly in ρ. Predator avoidance behavior affects ρ by directly limiting feedback loops through predation and thereby reducing those loops' contributions to multispecies density dependence. Likewise, because foraging activity may also be reduced by avoidance behavior, the contributions of resource consumption to ρ may also be reduced. However, for avoidance behavior to be adaptive, the benefit from reduction of predation must exceed the cost of reduction of resource consumption. We measure the degree to which it does this with the quantity $1 - f/g$ (effectiveness of avoidance), where f and g are, respectively, the ratios of predation and resource consumption with avoidance behavior relative to no avoidance behavior. Whenever avoidance effectiveness is nonzero—that is, whenever there is a greater proportional reduction of predation compared with resource consumption—the relative weight of predation in the overlap measure ρ is reduced, and predation has less influence on niche overlap. As the effectiveness of avoidance changes from 0% to 100%, the impact of predators on niche overlap declines to zero, and ρ then has exactly the same value that it has without predation. If the focal species strongly partition resources and are preyed on by a generalist predator (fig. 1*c*), effective avoidance decreases niche overlap and so increases the potential for coexistence (figs. 2*c*, 4*c*). If the opposite is true, such that the focal species compete strongly for the same resources but are limited by specialist predators (fig. 1*a*), then 100% effective avoidance behavior increases their niche overlap and shrinks the potential for coexistence (figs. 2*a*, 4*a*).

In contrast to the effectiveness of avoidance behavior, the intensity of avoidance behavior—defined by reducing g while maintaining a constant f/g ratio—affects only average fitness and not niche overlap (comparison of eqq. [11], [12]). Greater investment in avoidance behavior as measured by lost foraging opportunity causes differences in the κ_1/κ_2 to increase rapidly as foraging gains shrink toward the base metabolic rate m for each species (fig. 5). The difference between each species' m relative to the difference in foraging gains and predation losses,

Table 2: Summary of predator avoidance behavior's effects on coexistence

Avoidance	Effect on niche overlap	Effect on average fitness ratio
Effectiveness	Eliminates effect of predators: ρ convergences on the value based solely on resources	Equalizing when the species with higher H/m is disadvantaged without avoidance; otherwise greater effectiveness favors exclusion
Intensity	No effect	Promotes exclusion when the species with higher H/m also has an advantage without avoidance, otherwise equalizing over some range before ultimately approaching infinity or zero

$H - \mu$, is the critical determinant of which species can afford to avoid predators more intensely (eq. [16]).

Average fitnesses include the direct mortality that predators have on the focal species, and this is naturally reduced by effective avoidance. However, the costs of avoidance through reduced foraging also decrease average fitnesses. That is, even when predation is completely avoided, the limiting κ_1/κ_2 are still affected by predators because of the time spent avoiding them and not foraging (eq. [13]). When metabolic costs differ between species relative to their overall foraging abilities, the average fitness ratio in general will be affected by the presence of the predators even though there are no consumptive effects. Exceptions occur when avoidance behavior scales in proportion to relative harvesting ability, as can be seen from equation (14). Then there is no effect of predators on coexistence in the presence of even highly effective avoidance, provided avoidance behavior remains adaptive for each species. These conditions define when no effects of predation, whether consumptive or nonconsumptive, affect species coexistence. Deviations from these conditions define when predation continues to affect species coexistence even though avoidance behavior is highly effective.

Although we discuss the effects of intensity and effectiveness of avoidance behavior separately, they clearly are likely to interact in their effects on average fitnesses. For example, in guilds with very effective predator avoidance behavior, the difference between net harvest gains and maintenance requirements, $H - m$, will be of primary importance in determining which species benefits from more intense avoidance. On the other hand, with less effective avoidance, the species' minimum predation losses without avoidance, μ, factor more importantly into which species benefits from more intense avoidance.

Although we have considered only the interactions between two consumer species, the general thrust of our findings is independent of the number of species because the calculations of the key quantities κ's are the same regardless of the numbers of species, and ρ's are calculated on species pairs independent of how many other species are present. Moreover, these quantities are sufficient to define the dynamics of all n species (Chesson 2018). The complication in the n species case is not a change in the definition of any of the key parameters but the presence of indirect interactions between consumer species. This means that it is not sufficient for intraspecific competition to be merely greater than interspecific competition for coexistence to occur but a stronger requirement on the ratios of interspecific competition to intraspecific competition (Chesson 2018). Regardless, the changes in the key average fitnesses κ and niche overlaps ρ that feature in our two-species discussion here are independent of the number of consumer species.

In line with the effects we document for niche overlap, the review of Bolker et al. (2003) concluded that predator avoidance generally weakens the strength of apparent competition. This previous finding is consistent with our finding of a reduction in the contributions of predation to niche overlap as avoidance effectiveness increases. It is important to emphasize, however, that effectiveness of avoidance, not avoidance per se (e.g., as measured here by intensity of avoidance), is the critical quantity. The changes we predict in niche overlap and therefore effects on coexistence could be substantial, given that meta-analyses have found that nonconsumptive effects of predators can be as large as or larger than lethal predation (Werner and Peacor 2003). It is important to realize, however, that these empirical studies typically relate to intensity of avoidance, such as refractory period of sticklebacks (e.g., Alvarez and Bell 2007; Dingemanse et al. 2007), and not the effectiveness of avoidance, which is much more difficult to measure but more important for understanding coexistence. Effectiveness of avoidance would have to be measured for sticklebacks, for example, in terms of the reduction in mortality from heron attacks gained from hiding under a plant relative to the loss of feeding rate from hiding. Such tests could be conducted by comparing mortality and feeding rates of individuals from heron-naive pond populations with those in stream populations both with and without herons present.

Predator avoidance has also been incorporated into food webs of various topologies. Garay-Narvaez and Ramos-Jiliberto (2009) found that ultimately the effect of predator avoidance on the stability of three- to six-species systems was sensitive to the system, which is somewhat discouraging for finding general principles. Our results suggest a more general pattern within their analysis. Predator avoidance behavior that weakened apparent competition promoted community stability in topologies where other interactions were strengthened as a result but destabilized communities in which it did not strengthen nonfocal interactions. Our results suggest that the topologies in which stability was promoted were those in which the focal prey were ecologically distinguished by resource consumption rather than vulnerability to predation, because then niche overlap would be reduced by avoidance behavior.

The general principle that predator avoidance causes niche overlap to depend more heavily on resource overlap also applies to metacommunity models, in which the prey compete for seemingly interchangeable patches of habitat and predator avoidance results in increasing dispersal rates when predators are present (Orrock et al. 2008). The primary mechanism of coexistence without the predator in this model is a competition-colonization trade-off, and predator avoidance has been modeled as modifying the strength of that mechanism by altering colonization rates (Orrock et al. 2008). When increased colonization due to predator avoidance outweighs losses to predators through local extinctions, avoidance behavior can allow the persistence of an inferior competitor that would otherwise be driven extinct (Orrock et al. 2008). Our

analysis highlights the idea that predator avoidance in the metapopulation model could promote coexistence through altering the partitioning of even identical habitat patches, as they are differentiated by whether they are occupied by the predator or another species. Therefore, the changes in extinction and dispersal rates due to predator avoidance could stabilize coexistence by providing a greater role of habitat partitioning.

More of the previous work on predator avoidance has focused on the intensity or effectiveness of predator avoidance that is optimal and therefore likely to evolve (e.g., Abrams 1993, 2000; Matsuda and Abrams 1994; Abrams and Matsuda 1996, 1997; Abrams and Schmitz 1999; Abrams and Chen 2002*b*; Abrams and Vos 2003; Bolnick and Preisser 2005). The optimal levels of predator avoidance may be heavily dependent on specific parameters or features of a system, such as whether predators are detectable or predictable (e.g., Beckerman et al. 1997). In an adaptive dynamics framework without any ecological differentiation through resources or predators, predator avoidance can promote coexistence only if it reduces niche overlap by providing some ecologically differentiating tradeoff (Abrams and Matsuda 1993). Two species that coexist without predation because of low resource overlap, however, can evolve parallel avoidance behavior to a single shared predator (Abrams and Chen 2002*a*). These species still coexist with avoidance behavior if they experience greater intra- to interspecific density dependence through resources than due to predation, maintaining sufficient overall niche partitioning. Under scenarios of very high resource overlap, the avoidance strategies diverge as they evolve, which creates predator partitioning that could allow them to coexist (Abrams and Chen 2002*a*). The example of diverging rodent strategies (Kotler et al. 1994) may be explained by such strategy divergence. We have sidestepped the issue of what is optimal behavior here by exploring the effects of avoidance on coexistence over a greater range of behavioral effectiveness likely corresponding to a range of assumptions determining different optimal behaviors, which may be constrained by other selective forces on a suite of linked behaviors anyway (Conrad et al. 2011). In any case, optimality can be determined in our model only by adding more assumptions, with the outcomes likely specific to those assumptions.

Future Directions

There is now a substantial body of empirical literature demonstrating the prevalence and importance of avoidance behavior in predator-prey interactions across many ecological communities (Werner and Peacor 2003; Preisser et al. 2005). This model could similarly apply to any set of animals that hide in resource-poor refuges for some proportion of the time in which they would otherwise be foraging (e.g., Leibold 1991; Levri 1998; Katz et al. 2010). Moreover, it could apply to animals that reduce movement rates to avoid detection (Peacor and Werner 1997), that switch to less palatable resources available in safer locations than the preferred resources (Ovadia and Schmitz 2002; McArthur et al. 2012), that are more vigilant while grazing (Elgar 1989), or that concentrate their activity such that per capita access to resources is reduced (Elgar 1989), as these scenarios are often structurally indistinguishable in a mathematical model (Bolker et al. 2003).

In this context, our theoretical results provide predictions about the effects of this behavior on coexistence that can be tested in microcosms and the field. The most general prediction is that the more effective the avoidance behavior becomes, the stronger the effects of resource partitioning and harvesting abilities become in determining coexistence relative to predator partitioning and vulnerability. This effect could be quantified in the field using environmental manipulations to alter avoidance effectiveness and resource partitioning. Manipulations for studying this in the case of sticklebacks might include supplementing resources in existing refuge areas, for example, by adding blood worms to plant-covered reaches of streams to increase the effectiveness of avoidance for sticklebacks. Accessibility to the structure containing the food could be used to manipulate resource partitioning. Manipulations could also include providing additional refuges, such as artificial shelters for the fish with or without resources, as has been done in rodent studies (Orrock et al. 2015). These manipulations could be used to test hypotheses quantifying rates of individual vital rates in sticklebacks, whose generation time is only 1 year, or even follow populations for multiple generations to quantify the eventual outcome on their coexistence.

Future theoretical work should consider avoidance behavior that is sensitive to the abundance of predators and of resources. Although fixed degrees of avoidance behavior in the presence of predators may capture the dynamics of some systems well, such as grasshoppers avoiding birds (Belovsky et al. 2011), it is a restricted case. Many animals and even plants (Strauss et al. 2002) have developed predator avoidance strategies that scale in intensity with detected predator density (Peacor and Werner 1997), especially in situations where animals can detect their predators visually (Abramsky et al. 1997) or chemically (Peacor and Werner 1997). Additionally, resource availability can affect the level of investment in predator avoidance behavior (Bolnick and Preisser 2005; Preisser et al. 2009): a starving animal is more likely to accept greater predation risk (Brown and Kotler 2004; Werner and Peacor 2006). Considering more sensitive investment levels of avoidance behavior would likely alter the average fitness difference of the two species and may alter the responsiveness of niche overlap to predator avoidance effectiveness. Future work on these general models should investigate how that flexibility alters these results.

Conclusions

Although predation is often viewed in the ecological literature primarily as promoting coexistence by reducing the strength of competition (e.g., Gurevitch et al. 2000; Chase et al. 2002), predation causes apparent competition, which is a form of density dependence that can make up for or even exceed any reduction in density dependence from competition (Chesson and Kuang 2008). Coexistence depends on the relative strengths of intra- and interspecific density dependence, combining both competition and apparent competition, and we demonstrate here that predator avoidance behavior alters the relative strengths of density dependence through predators and resources. When predator avoidance behavior is very effective and not costly, resource use determines coexistence, as we have seen here in the two-species case through the niche overlap measures and average fitness ratios, which are then primarily reflective of resource use. The average fitness ratio may also change with avoidance effectiveness on the basis of which species' avoidance is more effective. Changes in the average fitness ratio due to avoidance effectiveness interact with changes in avoidance intensity, which benefit the species that can afford to forage less. These findings generalize to a wide range of systems in which a guild of similar species compete for resources and are vulnerable to predators, as does the underlying model of this system by Chesson and Kuang (2008). Given the importance of predator avoidance behavior on prey abundance (Abrams and Vos 2003; Abrams 2008), population growth rates (Preisser and Bolnick 2008), and persistence (Abrams 2000; Bolker et al. 2003; Mowles et al. 2011), a general theoretical understanding of coexistence is strengthened by incorporating this behavior. A greater focus on how altering the strength of a given interaction results in changes to community structure rather than solely on the interaction strength itself will further our future understanding in this area.

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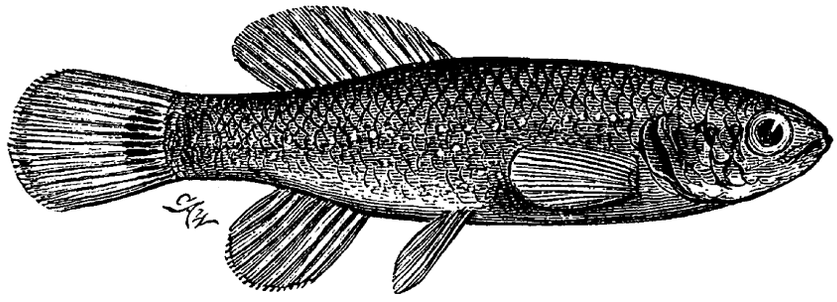

"Much is lost to those who essay to study the habits of fresh-water fishes, first, by avoiding uninviting mud-holes, and secondly, by walking carelessly to the banks of the stream, and seeing nothing at first, think they are themselves unseen by anything inhabiting the water. Never was there a greater mistake!" Figured: "Mud Minnow (*Melanura limi*)." From "Mud-Loving Fishes" by Charles C. Abbott (*The American Naturalist*, 1870, 4:385–391).